Methods of studying fish feeding: reply[1]

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Dietary descriptions of fish and other aquatic vertebrates are greatly influenced by the choice of the method used to quantify the relative importance or contribution of each prey type to the diet. This is because the most commonly used measures (numerical abundance, frequency of occurrence, and volume or weight measures) convey different types of information on feeding habits (Macdonald and Green 1983; Bigg and Perez 1985; Cortés 1997). This limitation of single indices led Pinkas et al. (1971) to propose the index of relative importance, or IRI, a compound index that describes the relative contribution of stomach contents to the diet. In a recent paper (Cortés 1997), I proposed to include the IRI standardized to 100% (%IRI), in addition to reporting the three single measures, *to facilitate comparisons between dietary studies*. Hansson argues that the IRI should be abandoned overall because it underrepresents lower taxonomic categories as shown in a hypothetical example.

Some of the limitations and biases of the single measures and some compound indices have been discussed elsewhere (Pinkas et al. 1971; Hyslop 1980; Macdonald and Green 1983; Bigg and Perez 1985). I argued that all three single measures should be reported when attempting to describe diets of populations or species because use of only one or two of them can be misleading (Fig. 2*b* in Cortés 1997 illustrates this point). Ideally, energy value of the prey should also be included as a measure of dietary importance, but this is beyond the scope of most studies. In his comment, Hansson shows that the IRI has limitations when attempting to quantify stomach contents from a single study because of the multiplicative effect that %*O* has on the index, with the net result of underestimating the contribution of those prey species identified to a lower taxonomic level. Although this is a valid point, I contend that the value of %*O* used in his example greatly influences the outcome, as recognized by Hansson. Before completely ruling out the use of IRI in dietary studies, its suitability and, by extension, that of all compound indices should be investigated further with examples drawn from multiple real data sets. As also pointed out by Hansson, conclusions should be based on numerical or statistical analyses, rather than on personal preferences or limited testing of hypothetical examples.

My recommendation of using %IRI responded more to a need to promote consistency and facilitate comparisons (Cortés 1997) than to a strong advocacy for compound indices. Indeed, I proposed to depict all three single measures graphically to easily visualize the importance of each food category in stomach content analyses. However, when making intra- or inter-specific comparisons, such as in calculations of dietary overlap, dietary breadth, or trophic levels, use of %IRI as a standardized measure can be useful despite the bias associated with this measure. In my opinion, it is preferable to using a single index because %IRI is an individual metric that integrates all three single measures, each of which can lead to misleading interpretations when used separately. For example, use of %N only to describe the diet of the blue shark would give the false impression that crustaceans are by far the most important item (Fig. 2*b* in Cortés 1997). In contrast, %IRI also considers contributions in weight and occurrence, thus emphasizing more the importance of cephalopodian molluscs and teleost fishes in the diet, which is more accurate (as determined in numerous studies of blue shark diets). Furthermore, if another study of blue shark diet were to use only %O or %W, for example, comparisons would be hindered because %N and %O or %W are not directly comparable. By combining the three single indices, %IRI puts results into a common metric, more amenable for use in diet comparisons and calculation of other trophic measures.

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